Biological Conservation 316 (2026) 111738

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Short communication

Wildfire smoke reduces the vocal activity of imperiled grassland birds in New York State

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ARTICLE INFO

Keywords:
Animal behavior
Bioacoustics
Global change ecology
Avian vocalization
Grassland birds
Wildfire ecology

ABSTRACT

Smoke from new fire regimes driven by climate change may affect biodiversity in new regions of the world. Wildfires that occurred in eastern Canada in 2023 burned nearly 7.8 million hectares of forest, sending smoke throughout the northeastern United States. We leveraged passive acoustic monitoring to investigate real-time effects of wildfire smoke on vocalization behavior of globally imperiled grassland birds during the breeding season in open land covers across New York State. We determined an overall negative effect of elevated smoke levels on breeding grassland bird vocal activity. We observed the strongest vocalization responses in Bobolink (*Dolichonyx oryzivorus*) – a colonial breeding, grassland-obligate species; Bobolink vocal activity sharply dropped during intense smoke early in the breeding season, yet increased during a milder smoke event later in the breeding season. Our results indicate that wildfire smoke can present an additive stressor to already imperiled grassland bird species via potential fitness reductions from decreased communication. While some aspects of smoke exposure may be uncontrollable, our results suggest that increased attention to conservation practices that promote grassland birds in the Northeast could be prioritized to offset negative effects of increased smoke associated with global change.

1. Introduction

Climate change and habitat loss are two of the greatest threats to biodiversity globally (Hogue and Breon, 2022). Climate change also contributes to increased wildfire severity and frequency across landscapes via widespread and rapid changes in land-use activities and climate-related factors, including rising temperatures, decreased precipitation, and extended fire seasons (Abatzoglou and Williams, 2016; Mueller et al., 2020; Radeloff et al., 2023; Williams et al., 2019). Climate change-fueled wildfires are rapidly accelerating landscape conversion and habitat loss for many species (Coop et al., 2020; Jones et al., 2022). Large wildfires can also impact human and wildlife health through exposure to temperatures and toxic smoke (Burke et al., 2021; Engstrom, 2010; Erb et al., 2023; Kala, 2023; Nihei et al., 2024).

Despite an increase in wildfire activity and associated smoke pollution, research on effects of wildfire smoke on wildlife is limited, partly due to challenges of concurrently measuring smoke conditions and wildlife responses in real-time during smoke events (Sanderfoot and Gardner, 2021). However, studies have addressed the influence of wildfire smoke on aspects of animal behaviors. Lee et al. (2017) found that, during record-setting smoke events in Southeast Asia, dawn acoustic activity associated with ecological communities dramatically decreased, with effects persisting for several weeks. Similarly, in the western United States, smoke exposure was associated with changes in soundscapes during and after smoke events (Sanderfoot et al., 2024). Research also has shown that orangutans reduce both movements and vocalizations during smoke events, highlighting strong behavioral responses to degraded air quality and possible implications for wildlife health (Erb et al., 2018, 2023). Wildlife responses to smoke exposure may be temporally variable; for example, Nihei et al. (2024) found that bird capture rates declined during acute smoke exposure but increased under more frequent smoke regimes. While these studies exemplify interactions between smoke exposure and animal sounds, studies targeting animal vocalizations during peak breeding season, when

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https://doi.org/10.1016/j.biocon.2026.111738
Received 25 March 2025; Received in revised form 27 September 2025; Accepted 3 February 2026
Available online 19 February 2026
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communication is paramount for fitness, are underrepresented across taxa (Carlson et al., 2020; Lassandro et al., 2025; Odom et al., 2021).

Bird vocalizations are important behaviors during the breeding season; they play roles in mate attraction, territory defense, and parent-offspring interactions (Catchpole and Slater, 2008). Anthropogenic disturbance can mechanistically influence bird vocalizations via changes to the sensory environment (Kight and Swaddle, 2011), disruptions to inter- and intra-specific interactions (Francis et al., 2009), and physiological stress (Nihei et al., 2024). Avian vocal activity can be reduced in response to increased anthropogonic noise levels in grasslands (Curry et al., 2018) and shrublands near wind facilities (Gómez-Catasús et al., 2022). Previous research has also suggested that elevated smoke levels may influence bird behavior and activity (Lee et al., 2017; Sanderfoot et al., 2024; Nihei et al., 2024). Employment of acoustic recording units has allowed for measurements of bird response to smoke without human-induced sampling bias in montane systems (Sanderfoot et al., 2024); our research employs acoustic monitoring during smoke events occurring during peak breeding season in grassland environments with unique soundscapes (Gómez-Catasús et al., 2022), smoke plumes (Junghenn Noyes et al., 2022), and fire regime (Malamud et al., 2005). Furthermore, smoke exposure is no longer limited to fire-prone regions; rather, it can be a widespread ecological stressor capable of affecting species far beyond the source of the wildfire (Overton et al., 2021).

In northeastern North America, fire regimes are relatively understudied, leaving the ecological consequences of increased wildfire and associated smoke uncertain (Dems et al., 2021; Malamud et al., 2005; Salguero et al., 2020). Although large-scale wildfires in the northeastern United States (U.S.) are novel, climate change is expected to increase their frequency (Gao et al., 2021; Wang et al., 2022). Record-breaking wildfires occurred in eastern Canada during the summer of 2023, burning nearly 7.8 million hectares of forest and significantly impacting air quality throughout the northeastern U.S. (Kolden et al., 2024; MacCarthy et al., 2024). Smoke generated from these fires offered a unique opportunity to study consequences of changing smoke regimes on imperiled species already facing multiple anthropogenic threats, such as rapidly declining grassland birds (Hogue and Breon, 2022).

Grassland ecosystems are rapidly being lost across North America (Carbutt et al., 2017; Knopf and Samson, 1997), causing severe declines in grassland bird populations (Brennan and Kuvlesky, 2005; Shriver et al., 2005). In North America, grassland birds have undergone the most dramatic population declines of any avian guild in the last 50 years (Rosenberg et al., 2019), with climate change further exacerbating the trend (Stein et al., 2018). Losses in grassland bird populations have been observed in the northeastern U.S., where shifts in land use over recent decades—particularly agricultural abandonment and changes in agricultural practices such as hay production—have contributed to the decline in grasslands and subsequently grassland birds (Murphy, 2003; Peterjohn and Sauer, 1999). Consequences of altered fire regimes, such as increased fire severity and extent as well as increased smoke concentrations, on grassland birds are unclear and likely regionally variable (Arrogante-Funes et al., 2024). Indeed, fire is a common feature of some grassland systems (e.g., Great Plains, U.S.; Roberts et al., 2022), however less is understood about fire-wildlife interactions in grasslands of the northeastern U.S.

Here, we leveraged passive acoustic monitoring to investigate near real-time effects of wildfire smoke on the vocal behaviors of grassland birds during the breeding season. We assessed these effects for grassland-obligate and generalist birds of open habitats with variable distributions (i.e., eastern U.S. versus continental) during pronounced smoke events stemming from the eastern Canada wildfires in 2023. We predicted that avian vocal activity rates would be negatively associated with smoke concentrations across all species, due to physiological and behavioral stressors (Cascio, 2018; Erb et al., 2023). We also predicted that relationships between vocal activity and smoke concentrations would differ by species-specific life history traits, including habitat association (i.e. grassland-obligate or generalist species) and distribution (i.e. widespread or eastern-restricted species) (Jager et al., 2021). Finally, we predicted that there might be a threshold of smoke exposure above which the impacts on vocal behaviors become most apparent, as species struggle to cope with the most elevated smoke concentrations.

2. Materials and methods

2.1. Focal avian species

We selected eight focal species that occur in grasslands and grassland-like land covers in the eastern U.S., including grassland-obligate species and species that represent variable habitat specialization and continental distributions. We selected species that breed in New York State during the summer and use vocalizations in territory establishment and defense, mate attraction, and communication with offspring. We selected three generalist species, Red-winged Blackbird (*Agelaius phoeniceus*), Common Yellowthroat (*Geothlypis trichas*), and Song Sparrow (*Melospiza melodia*); one facultative grassland species, Field Sparrow (*Spizella pusilla*); and four grassland-obligate species, Bobolink (*Dolichonyx oryzivorus*), Savannah Sparrow (*Passerculus sandwichensis*), Eastern Meadowlark (*Sturnella magna*), and Horned Lark (*Eremophila alpestris*) (Arcese et al., 2020; Beason, 2020; Guzy and Ritchison, 2020; Wheelwright and Rising, 2020; Yasukawa and Searcy, 2020). Of these, three species (Bobolink, Eastern Meadowlark, and Field Sparrow) have ranges restricted to the eastern half of North America, while the remaining species have continental distributions (Carey et al., 2020; Jaster et al., 2022; Renfrew et al., 2020).

2.2. Passive acoustic surveys

As part of a larger project monitoring grassland ecosystems in New York State, we conducted passive acoustic surveys during the 2023 breeding season at 45 sites, including federal and state conservation areas managed under Best Management Practices for grassland birds, as well as extensive unprotected grassland habitats on private lands, including hay, pasture, alfalfa, corn, and soybean fields (NYSDEC, 2022). Surveys were designed to evaluate the effectiveness of grassland bird management and protection efforts in New York State by measuring grassland bird community assemblages and relative population sizes of species of conservation concern. The distance between survey sites averaged approximately 30 km (Fig. 1). We deployed one autonomous recording unit (ARU; SwiftOne Recorder, K. Lisa Yang Center for

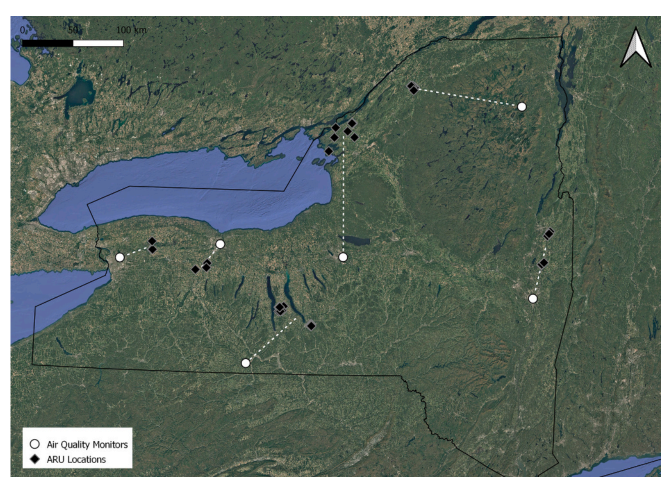

Fig. 1. Locations of Acoustic Recording Units (ARU) and Air Quality Monitors in New York State. Data collected from each ARU was spatio-temporally related to air quality data collected from the nearest (Euclidean distance) Air Quality Monitor (dotted white lines).

Conservation Bioacoustics) at each survey site.

ARUs were mounted on channel posts at a height of 1.5 m above ground level. We programmed ARUs to record daily when birds are most active between 04:00 and 11:00 (local time) from May to August 2023, using omnidirectional microphones and a sampling rate of 48 kHz to capture the full frequency range of avian vocalizations. For analysis, we used only the recordings from the date of 1 June 2023 to 10 July 2023 (40 days), thereby excluding the pre-territory establishment and post-fledging periods and focusing on peak breeding season vocal activity of our focal species (SI Fig. 1). We identified vocalizations of focal species from acoustic data using the BirdNET algorithm (Kahl et al., 2021). For each species, we manually validated 150 BirdNET predictions, which were randomly selected from across our entire acoustic dataset and fit a logistic regression relating BirdNET's prediction scores (a relative measure of algorithm confidence) to the binary outcome (i.e., correct/incorrect) (Wood and Kahl, 2024). We then solved each species equation for the confidence score required to achieve a probability of correct prediction of $\geq$0.80. We also used the 150 validated BirdNET predictions to calculate *precision* (the ratio of true positive predictions to the total number of predictions), *recall* (the ratio of true positive predictions to the total number of target signals), and *F1 score* (the harmonic mean of precision and recall) for each species (He and Ma, 2013). We used these metrics to evaluate the relative performance of the BirdNET algorithm in making species-specific vocalization predictions (see Table 2 and SI Fig. 2) (Priyadarshani et al., 2018; Sethi et al., 2024; Stowell, 2022; Wood et al., 2021). We retained BirdNET species predictions above our species-specific validation thresholds as observations in subsequent analyses. From these observations, we calculated the total daily vocalizations for each species at each site.

2.3. Environmental covariates

We represented smoke from wildfire based on a measure of fine particulate matter with an aerodynamic diameter <2.5 μm ($PM_{2.5}$); which is widely accepted as a proxy for smoke exposure and has been successfully used to evaluate effects of smoke on birds (Cascio, 2018; Erb et al., 2023; Lee et al., 2017; Sanderfoot et al., 2024; Sanderfoot and Gardner, 2021; Wettstein et al., 2018). We obtained daily average $PM_{2.5}$ measurements from the Environmental Protection Agency (EPA) Air Quality System (U.S. Environmental Protection Agency 2023; https://www.epa.gov/outdoor-air-quality-data). We selected Air Quality Monitors that comply with the National Ambient Air Quality Standards and the Federal Reference Method (FRM) (Sanderfoot and Gardner, 2021; U.S. Environmental Protection Agency (EPA), 2019) and paired the acoustic measurements from each ARU with air quality measurements from its nearest (Euclidean distance) EPA ground-based Air Quality Monitor (AQM) (Fig. 1). We also calculated Haversine (Great-Circle) distance between each ARU and its paired AQM and included this distance as a site-level covariate in our models to account for potential differences in smoke conditions between ARU and AQM locations. The distance between ARUs and paired AQMs ranged from 22 to 185 km (median = 68 km). To validate the exposure estimates at ARU sites based on nearest AQM measurements, we assessed an alternative measure of $PM_{2.5}$: NASA's Hazardous Air Quality Ensemble System (HAQES) of mean surface total of $PM_{2.5}$ concentration over the continental United States (Makkaroon et al., 2023; Tong, 2023) (see SI Eq. (2)). We found a high, positive correlation between the value of AQM $PM_{2.5}$ measurements and values from the HAQES model (r = 0.72, n = 1800, p-value <0.001). Additionally, we re-ran all statistical models described below (see Statistical analysis) replacing AQM $PM_{2.5}$ measurements with values from the HAQES model and removing the variable of ARU-AQM distance. Models using HAQES estimates did not differ substantially from models using ground-based estimates and distance offsets (SI Table 2 and SI Table 3). Thus, we chose to retain ground-based estimates and distance offsets in our final models, due to the greater reliability of ground-measures compared to modeled conditions (Makkaroon et al., 2023).

Within the peak grassland bird breeding season, we identified "smoke events" as date ranges with $PM_{2.5}$ levels exceeding 40 μg/m^3 (24-h average) and corresponding Air Quality Index scores above 100, a threshold that triggers statewide alerts for adverse air quality conditions of immediate concern for human health and wellbeing. Because thresholds for negative impacts of $PM_{2.5}$ levels on birds remain unknown, we used human health standards as guidance for classifying smoke events; we assumed that bird susceptibility would be similar to humans or greater at such smoke levels, given birds' higher aerobic capacity and faster metabolic rates (Gill, 2007; Sanderfoot and Holloway, 2017). Based on these criteria, we detected two major smoke events during the 40-day peak avian breeding season: Smoke Event A, 5 June 2023 to 8 June 2023 (average $PM_{2.5}$ = 76 μg/m^3, average AQI = 136); and Smoke Event B, 28 June 2023 to 1 July 2023 (average $PM_{2.5}$ = 50 μg/m^3, average AQI = 120) (Fig. 2). Both smoke events spanned all AQM and ARU locations (SI Figs. 3 and 4). For each smoke event, we analyzed data for a 12-day period, consisting of four days preceding the onset of elevated smoke levels, four days during peak $PM_{2.5}$ concentrations (above 40 μg/m^3), and four days following a decline in smoke levels. Given the known relationships among avian activity, precipitation, and temperature (Santillán et al., 2018), we obtained data from the PRISM Climate Group gridded dataset (Oregon State University, http://www.prism.oregonstate.edu) to calculate daily mean air temperature (°C) and accumulated precipitation (mm) for a 4 km × 4 km grid cell in which ARU site occurred. We paired this data with daily average $PM_{2.5}$ across the 40-day breeding season.

2.4. Statistical analysis

2.4.1. Effect of smoke on avian vocalization rates during peak breeding season

We used a Generalized Additive Model (GAM; Gaussian distribution, identity link function) using the *mgcv* R package (R Core Team, 2024; Wood, 2011) to analyze effects of environmental conditions, location, and date on daily vocalizations throughout the peak breeding season (40 days) of all focal species combined. To improve numerical stability, we mean-centered and scaled all numeric predictors: $PM_{2.5}$, precipitation (*ppt*), temperature (*t*), distance to the nearest AQM in meters (*d*), and Julian date (*date)*. We included $PM_{2.5}$ concentration as a linear term and modeled ARU site as a random effect. Because of the high concurvity of temperature, date, and precipitation, we modeled these variables jointly, allowing for nonlinear interaction using a tensor product smooth (*te*) with thin plate regression spline for temperature and precipitation, and cyclic cubic regression spline for the date to account for its cyclical nature. This approach provides flexibility in capturing seasonal patterns while controlling collinearity among predictors (Wood, 2017) (see SI Eq. (1)). Prior to inclusion, we evaluated the necessity of smoothing, using statistical diagnostics of model comparison (Chambers and Hastie, 1992) to ensure that the assumption of nonlinearity was supported by the data and whether the inclusion of date, temperature, and precipitation significantly improved model fit by comparing nested models (Zuur et al., 2009). Interactions between $PM_{2.5}$ and weather variables were not included in the final model as weather variables along with date were modeled as smooth terms, reducing potential for concurvity and redundancy and improving model fit (Wood, 2017).

2.4.2. Effect of smoke on species-specific vocalization rates during smoke events

We used generalized additive models to investigate species-specific vocalization rate responses to $PM_{2.5}$ levels and distance to nearest AQM in meters (*d*) during each smoke event, with site as random effect (see SI Eq. (3)). We used the slope from each model to evaluate the effects of $PM_{2.5}$ levels on the daily vocalizations of each species. We confirmed that the assumption of normality for each model was met by examining residual plots; variance was roughly constant across fitted

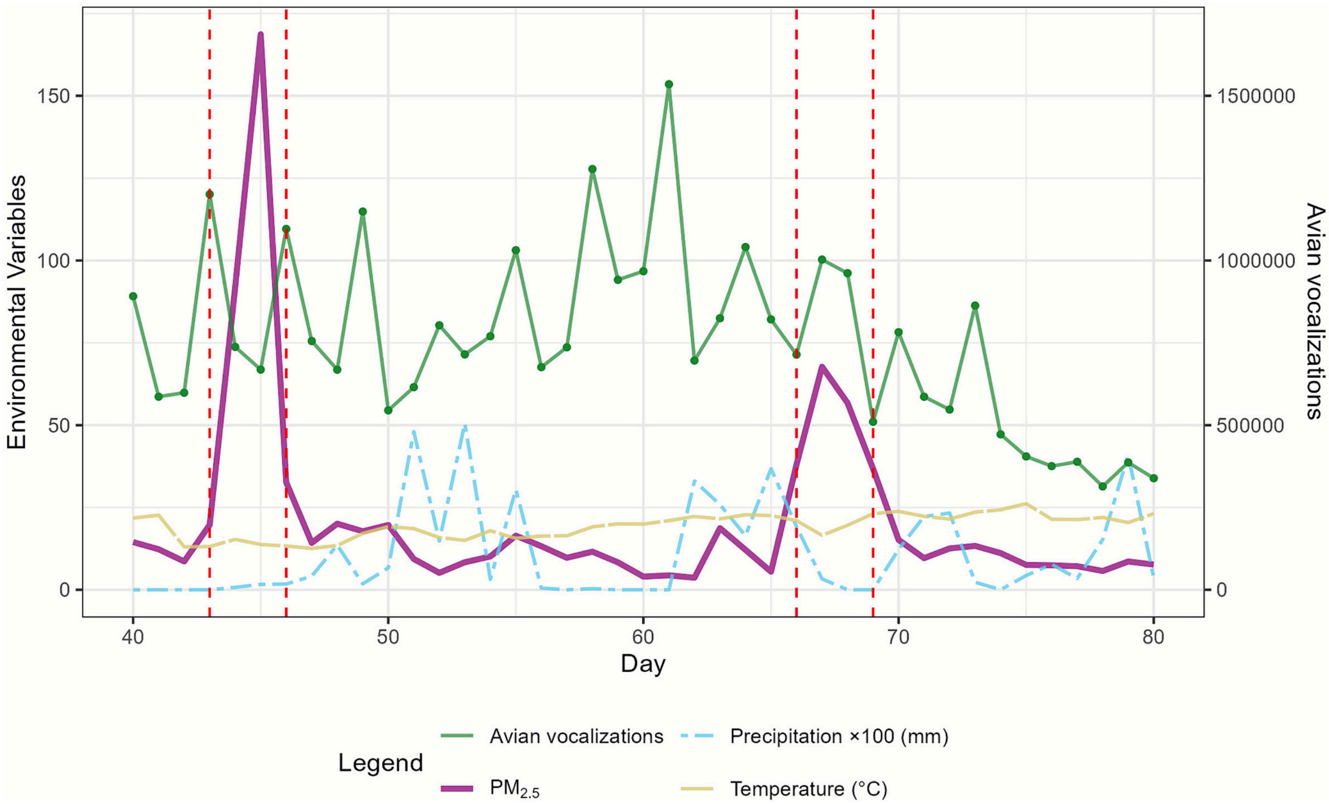

Fig. 2. Daily vocalizations of all focal species combined (green line), average daily $PM_{2.5}$ levels (purple line), average daily precipitation (mm; blue line, scaled by a factor of 100), and average daily temperature (^{0}C; yellow line) during the peak 40-day avian breeding season (1 June 2023 to 10 July 2023; daily vocalizations for the entire breeding season are included in SI Fig. 2). We defined smoke events as conditions with >40 μg/m^3 $PM_{2.5}$ and >100 Air Quality Index (USEPA, 2012), resulting in Smoke Event A, 5 June 2023 to 8 June 2023 (average $PM_{2.5}$ = 76 μg/m^3, average AQI = 136) and Smoke Event B, 28 June 2023 to 1 July 2023 (average $PM_{2.5}$ = 50 μg/m^3, average AQI = 120) (dashed vertical red lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

values, with no strong evidence of concurvity.

3. Results

3.1. Effects of smoke on avian vocalization rates during peak breeding season

We recorded 3,099,694 vocalization observations across eight focal species. We found significant, negative linear effects of $PM_{2.5}$ on the daily vocal activity of all focal species (Table 1, Fig. 3). Distance between ARUs and AQMs did not significantly influence vocal activity (Table 1). Effective degrees of freedom indicated strong, non-linear effects and interaction of temperature, precipitation, and date on avian vocal activity (adjusted R^2 = 0.60, n = 1346; Table 1; SI Fig. 5).

Table 1
Parameter coefficients for Generalized Additive Model of combined focal species' daily vocalizations. Asterisks indicate significant parameter effects, edf: effective degrees of freedom, ref.df: reference effective degrees of freedom, te = tensor product smooth, s = smooth function.

Significance of linear terms

Variables	Estimate	Std. error	t-value	p-value
(Intercept)	2117.06	158.57	13.351	<0.001***
$PM_{2.5}$	−240.40	42.21	−5.67	<0.001***
Distance	69.59	170.29	0.409	0.683

Approximate significance of smooth terms

Variables	edf	Ref.df	F- value	p-value
te (Temperature, Precipitation, Date)	51.66	60.88	5.79	<0.001***
s (Site)	42.56	44	31.779	<0.001***

3.2. Effects of smoke on species-specific vocalization rates during smoke events

Smoke Event A (5 June 2023 to 8 June 2023) was characterized by greater $PM_{2.5}$ levels (average $PM_{2.5}$ = 76 μg/m^3) than Smoke Event B (28 June 2023 to 1 July 2023; average $PM_{2.5}$ = 50 μg/m^3), though both smoke events were above dangerous thresholds for $PM_{2.5}$ (Fig. 1). All focal species demonstrated a negative relationship between vocalization rate and smoke levels during Smoke Event A (Fig. 3A); however, this relationship was not statistically significant for all species. No focal species exhibited significant reductions in vocal activity during Smoke Event B; however, Bobolink, Common Yellowthroat, and Field Sparrow displayed a significant increase in vocalization rate during Smoke Event B (Fig. 3B).

Among the obligate and facultative grassland bird species, all but one (Horned Lark) significantly reduced vocal activity during Smoke Event A (Fig. 3A; Table 2). Of the three generalist species, Common Yellowthroat and Song Sparrow significantly reduced vocal activity during Smoke Event A (Fig. 3A; Table 2). All three species with eastern distributions demonstrated significant declines in vocal activity during Smoke Event A, while only three of the five species with continental distributions did so during the same smoke event (Fig. 3A; Table 2). Bobolink demonstrated the greatest decline in vocal activity during the more intense Smoke Event A, followed by Savannah Sparrow, Common Yellowthroat, and Song Sparrow, all of which showed moderate reductions. ARU-AQM

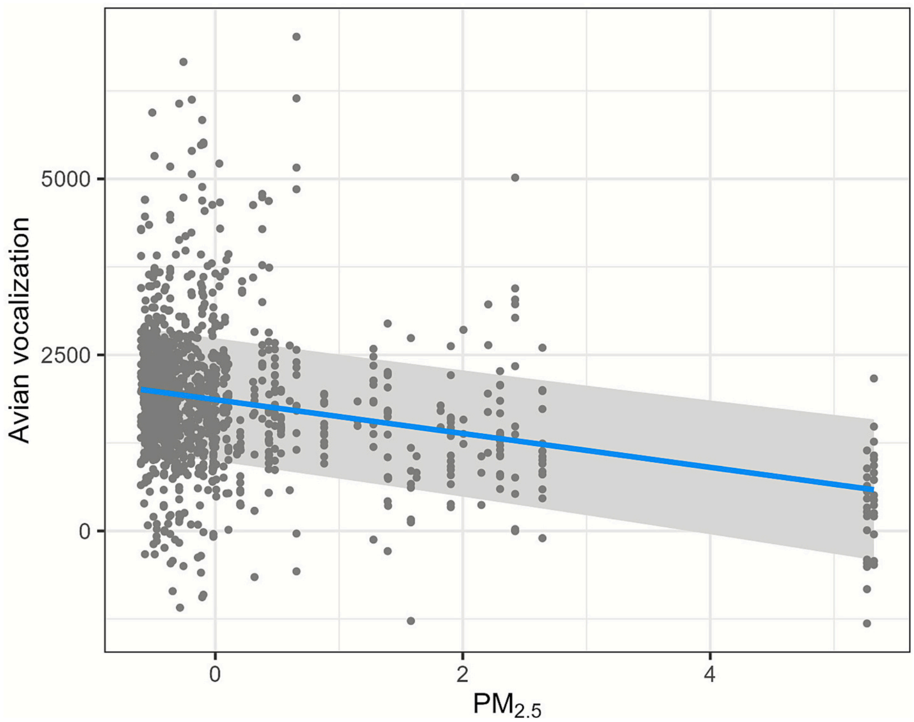

Fig. 3. Effect of $PM_{2.5}$ on combined species' total daily vocalizations. The linear term shows a significant decline in total vocalization with an increase of $PM_{2.5}$. Other linear and nonlinear terms of the model are included in the supporting information (SI Fig. 5).

Table 2
Parameter estimates and significance levels for models of the effect of $PM_{2.5}$ on the daily vocalizations of eight focal species during Smoke Events A and B. Species with *p*-values <0.05 or parameter estimates with 95% confidence interval not overlapping 0 are indicated by asterisks (*). BirdNET prediction performance metrics and the ecological attributes (primary habitat association and North American distribution) are included. The parameter estimates for the effect of the Distance (m) are included in the supplementary material (SI Table 1).

Species	Smoke Event A		Smoke Event B		BirdNET predictions performance metrics			Ecological attributes	
	$PM_{2.5}$ (*estimate*)	*(95% CI)*	$PM_{2.5}$ (*estimate*)	*(95% CI)*	Recall	Precision	F1-score	Habitat association	Distribution
Bobolink	−134.77	(−199.22, −70.32)*	189.55	(88.6, 290.5)*	0.8	0.98	0.91	Obligate	Eastern U.S.
Common Yellowthroat	−23.88	(−38.03, −9.74)*	80.12	(17, 143.23)*	0.9	0.97	0.95	Generalist	Continental
Eastern Meadowlark	−20.17	(−29.08, −11.25)*	38.69	(−13.18, 90.55)	1	0.95	0.98	Obligate	Eastern U.S.
Field Sparrow	−13.69	(−24.41, −2.96)*	61.24	(19.57, 102.9)*	1	0.95	0.97	Facultative	Eastern U.S.
Horned Lark	−0.38	(−2.26, 1.49)	−0.85	(−2.27, 0.58)	1	0.76	0.85	Obligate	Continental
Red-winged Blackbird	−7.92	(−16.19, 0.34)	−5.52	(−29.01, 17.96)	0.7	0.94	0.81	Generalist	Continental
Savannah Sparrow	−29.58	(−53.05, −6.1)*	69.07	(−55.67, 193.82)	0.8	0.92	0.83	Obligate	Continental
Song Sparrow	−21.45	(−38.22, −4.68)*	29.26	(−16.28, 74.8)	0.9	0.94	0.93	Generalist	Continental

distance was not a significant predictor of species' vocal activity in most (15 out of 16) models (SI Table 1). Recall rate and F-1 score were consistently high across species (Table 2), supporting the reliability of our findings and our ability to compare vocal activity between species (Fig. 4).

4. Discussion

We found an overall negative effect of elevated smoke levels on grassland bird vocalization behavior during the breeding season across New York State. Effects of wildfire smoke were additive to combined influences of temperature, precipitation, and date, all known to strongly influence avian vocal behavior (Santillán et al., 2018). Vocal activity was uniformly reduced across all focal species during the most intense smoke event of the 2023 breeding season, with significant reductions in five of eight species. However, vocal activity during a subsequent, less intense smoke event later in the season showed an overall increase, but insignificant responses to elevated smoke conditions. Thus, while vocal activity was generally negatively associated with smoke levels across the entire breeding season, there could be variable responses of avian vocalization to smoke at different stages of the breeding season or a threshold for smoke intensity effects on avian vocalization may exist. Furthermore, we found evidence for species-specific differences in vocal behavior responses to elevated smoke conditions. Grassland specialists, most significantly Bobolink, generally showed greater reductions in vocal activity under elevated smoke conditions compared to generalist species. Additionally, the proportion of species with eastern range distributions that demonstrated declines in vocal activity due to smoke was greater than that of species with continental range distributions, including the western U.S. where wildfires are more historically

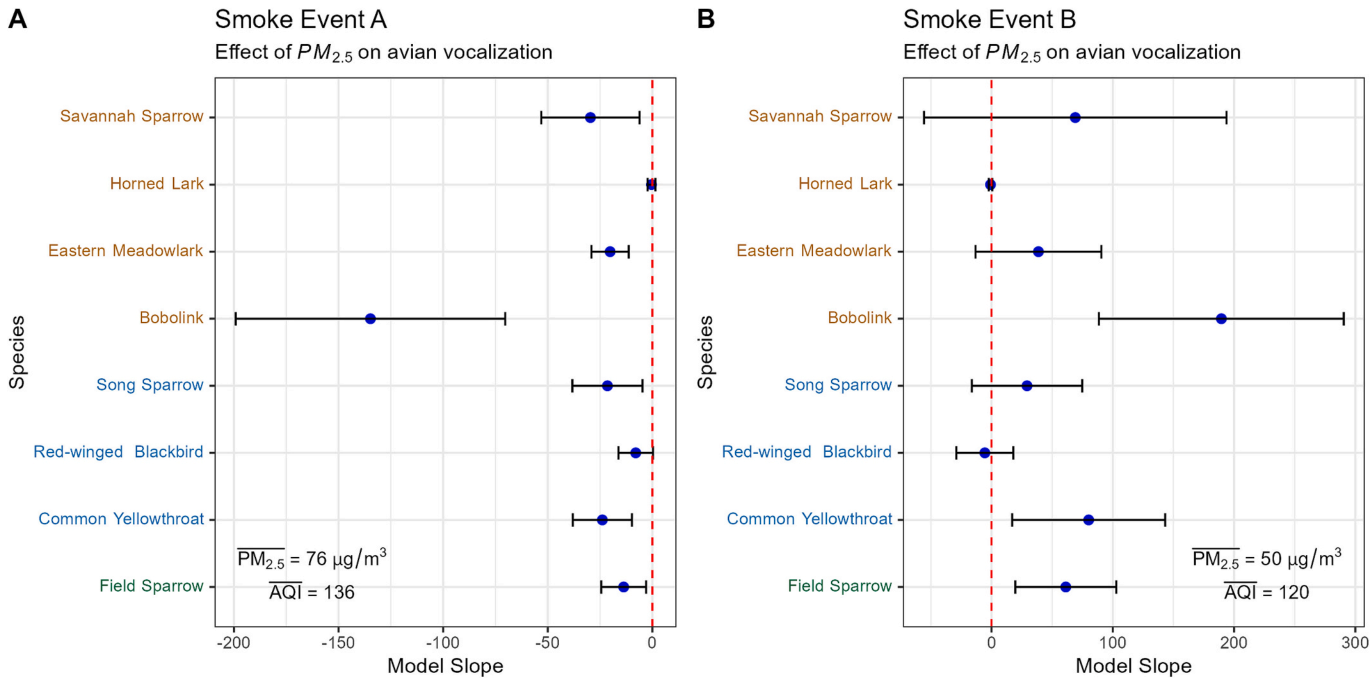

Fig. 4. Comparison of model slope estimates representing the effect of $PM_{2.5}$ on daily vocalizations of eight focal species. Each blue point and horizontal bar represent the estimated slope for each species (with 95% confidence intervals). Models for Smoke Event A (panel A) and Smoke Event B (panel B) are presented side-by-side. Negative slope estimates indicate reduced vocalization activity during smoke events, while positive slopes indicate increased vocal activity during smoke events. Grassland obligate species are indicated by yellow color font; generalist species are indicated by blue color font; facultative grassland species are indicated by green color font. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

common (Malamud et al., 2005).

Elevated smoke levels were associated with decreased vocalization rates across the full breeding season for all species combined, suggesting broad impacts of smoke exposure; however, differential avian responses to smoke events warrant exploration of potential mechanisms. Smoke Event A ($PM_{2.5}$ of 76) was more severe than Smoke Event B ($PM_{2.5}$ of 50), thus the negative effects of Smoke Event A on grassland bird vocalizations may be related to a threshold of smoke severity to incite vocalization response somewhere above a $PM_{2.5}$ of 50. Yet temporal aspects may affect this interpretation since Smoke Event A occurred during a different stage of the breeding season than Smoke Event B and avian vocal behavior can vary with breeding season stage (Lima, 2009; Vézina and Salvante, 2010). Smoke Event A coincided with territory establishment and mate attraction behaviors, when vocal activity is typically high (Arcese et al., 2020; Beason, 2020; Guzy and Ritchison, 2020; Wheelwright and Rising, 2020; Yasukawa and Searcy, 2020), while Smoke Event B occurred during nestling provisioning and juvenile guarding, when vocal activity typically declines as individuals shift to parental care behaviors (Renfrew et al., 2020; Jaster et al., 2022). Since Smoke Event B occurred after Smoke Event A, vocalization response to Smoke Event B may have been affected by the occurrence of Smoke Event A via adaptation, learned behaviors, or other mechanisms. For example, individuals may increase their vocal activity as part of securing sufficient resources to recover from sublethal health effects related to previous smoke exposure (Nihei et al., 2024).

Significant reductions in vocal activity during the breeding season may have consequences for grassland bird fitness and population trends. Reductions in vocal behavior could be indicative of declines in a broader suite of behaviors necessary for birds' ability to maintain access to resources, attract mates, and reproduce successfully (Barton et al., 2023; Kight and Swaddle, 2011; Richard et al., 2021; Sumasgutner et al., 2023). Additionally, reduced vocal activity could be indicative of physiological stress and adverse health effects in birds exposed to smoke (Nihei et al., 2024; Sanderfoot and Holloway, 2017). Smoke exposure may negatively affect individual birds' longevity and reproductive success, potentially leading to population-level effects. Such consequences could be particularly meaningful for grassland birds, where smoke exposure could pose an additional challenge to already imperiled species affected by habitat loss and other anthropogenic pressures (Côté et al., 2016). Relatively small population sizes of grassland bird species across patchily distributed grassland habitats of the northeastern U.S. might render them less resilient to novel stressors such as smoke through such mechanisms as reduced genetic diversity and limited capacity for adaptation (Eichenwald et al., 2020; Stockwell et al., 2003).

Our findings may be explained in part through the lens of possible eco-evolutionary mechanisms driving avian responses to smoke exposure. During the most intense period of elevated smoke conditions, we observed the most significant declines in vocal activity in species with ranges restricted to eastern North America. Conversely, species with continental distributions (including western ranges) generally did not exhibit strong negative associations between vocal activity and smoke levels. The restricted ranges of bird species in the eastern U.S. could imply an evolutionary history less intertwined with fire regimes compared to species with western distributions (Jager et al., 2021; Malamud et al., 2005; Salguero et al., 2020). In New York, wildfires, particularly forest fires, are rare and most grasslands are on agricultural lands where prescribed burns are largely absent or carefully timed to avoid the breeding season (NYSDEC, 2022). As such, the exposure of grassland birds to wildfire smoke in the northeastern U.S. could be a relatively novel phenomenon. While the number of species considered in this study is relatively few, future research could further investigate the role of fire exposure over evolutionary timescales in influencing species' responses to novel fire regimes (Coppedge et al., 2008; Haney et al., 2008; Mendelsohn et al., 2008). The most significant declines in vocal activity also tended to be observed in species that are either grassland-obligate or facultative grassland birds (i.e., Bobolink, Eastern Meadowlark, Field Sparrow, and Savannah Sparrow; Carey et al., 2020; Jaster et al., 2022; Renfrew and Saavedra, 2007; Wheelwright and Rising, 2020), bringing to light the potential susceptibility of grassland birds to regionally novel smoke events. Differing responses to smoke originating from forest fires (as compared to grassland fires) between grassland-obligate and habitat generalist species could be linked to limited evolutionary exposure to forest wildfire and smoke in grassland-obligate species (Arrogante-Funes et al., 2024; Malamud et al., 2005; Salguero et al., 2020). Additional studies incorporating larger geographic areas and more species could seek to investigate interactions between evolutionary history, contemporary life-history traits, and changes to fire regimes. Indeed, attention has recently been drawn to the importance of trait-fire mismatches, where the distribution of fire-related traits across and within species may interact with changing fire (and thereby smoke) regimes to render species – and entire communities – more or less adaptable to these environmental changes (Kelly et al., 2025).

Building off exploration of species-specific responses to smoke, our results indicate that colonial birds heavily reliant on vocal communication may be especially susceptible to effects of smoke exposure, but behaviors can vary over the breeding season. Indeed, we observed the greatest changes in vocal activity in Bobolink, a colonial breeding, grassland-obligate species of the eastern U.S. Bobolink vocal activity dropped sharply during peak smoke early in the breeding season but rose under milder smoke conditions later, suggesting shifting behavioral priorities and complex social responses to smoke exposure across the breeding season. Bobolink reliance on social communication may make them especially sensitive to novel environmental stressors. Similar susceptibilities of highly social animals to disturbance have been observed in other cases: Johnson et al. (2023) found Acorn Woodpeckers (*Melanerpes formicivorus*) reduce social connectivity and coordination on smoky days; Rubenstein (2007) showed that water availability affects cooperative interactions in Superb Starlings (*Lamprotornis superbus*); and Fisher et al. (2021) found that polluted environments can destabilize social systems in animals broadly. Environmental stressors like smoke may similarly disrupt behaviors for socially gregarious species, with potential consequences for reproductive success and population trajectories.

Previous research has often inferred, rather than directly measured, effects of elevated wildfire smoke on breeding bird behavior (Nihei et al., 2024; Sanderfoot et al., 2024). In contrast, our study directly measures the relationship between smoke conditions and species-specific behaviors in near real-time, providing additional evidence for direct effects. While passive acoustic monitoring allowed us to collect detailed information on bird vocal activity, obtaining localized measures of smoke conditions remains a challenge (Diao et al., 2019). By comparing ground-based $PM_{2.5}$ measurements with NASA HAQES-derived $PM_{2.5}$ modeled data, we utilized the most accurate and highest resolution estimates available. Yet, localized variation in smoke exposure may influence avian behavior across finer spatial and temporal scales than currently recognized (Nihei et al., 2024; Sanderfoot et al., 2024; Sanderfoot and Holloway, 2017). Further advances in both air quality and wildlife monitoring may offer new insights into these fine-scale behavioral responses; ARUs provide a good starting point to achieve this (Sanderfoot et al., 2024).

Our results indicate that wildfire smoke can negatively influence bird vocal activity, which may represent an additive stressor for imperiled grassland birds. Projections of increasing wildfire frequency and smoke intensity in eastern North America due to climate change (Burke et al., 2021; Jones et al., 2022; Salguero et al., 2020; Thompson et al., 2013) suggest increased smoke events that can interact with negative effects like agricultural abandonment in the region (Murphy, 2003; Peterjohn and Sauer, 1999). If, as our results suggest, smoke affects vocal behaviors critical for reproduction, imperiled grassland bird species could experience exacerbated population declines via decreased fitness. Importantly, our results show that effects of fire are not limited to localized land-cover changes; smoke exposure can extend hundreds of kilometers beyond burned areas, creating additional regional stressors. Further research is needed to examine the effects of elevated smoke levels on bird behavior, physiology, and ecology (Sanderfoot et al., 2021, 2024). Studies at local, regional, and global scales across suites of species can help determine the prevalence of wildlife smoke effects across scales and inform relevant conservation strategies for species. Our results do not necessarily pertain to prescribed fire as a grassland management tool, which may produce localized smoke effects that are relatively minor compared to the large-scale smoke impacts from uncontrolled forest wildfires driven by climate change (Jaffe et al., 2020; Long et al., 2022). While some aspects of smoke exposure may be uncontrollable, our results suggest that increased attention to conservation practices that promote grassland birds in the Northeast could be prioritized to offset negative effects of smoke.

CRediT authorship contribution statement

Trifosa I. Simamora: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Formal analysis, Data curation. **Timothy J. Boycott:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Connor M. Wood:** Writing – review & editing, Software, Resources, Methodology, Conceptualization. **Steven M. Grodsky:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

L. Crenshaw provided useful comments to improve the manuscript and L. Cheeley assisted in the processing of bioacoustics data. Funding to support this research was provided by the New York State Department of Environmental Conservation. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111738.

Data availability

Data will be made available on request.

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